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景观基因组学的研究进展及其在害虫综合治理中的应用

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摘要: 随着测序技术和生物信息学的快速发展,昆虫基因组学及其相关研究成果与日俱增。把农田景观要素嵌入基因组结构、适应性遗传变异和基因功能的研究,揭示在特定景观背景下害虫适应性和致害性的分子机理,是景观基因组学与害虫治理研究的新领域。景观基因组学是景观生态学与种群基因组学的交叉学科,旨在探究生物对所处环境适应性的遗传基础;研究重点是在环境因子的选择作用下,考察和分析物种的适应性进化及群体之间的基因流和遗传漂变;研究方法可以概括为空间采样策略的设计、分子标记的使用、数据的采集与分析。本文概述了景观基因组学的研究现状,包括近年来的主要研究发现和成果,并进一步阐述了景观基因组学在昆虫抗药性治理、保护性生物防控、全球气候变化背景下的害虫综合治理等方面的应用及前景,旨在促进更加有效地开展可持续的害虫综合治理,减少化学农药的使用,促进作物安全生产。

关键词: 景观基因组学; 遗传学; 适应; 进化; 转基因作物; 抗药性; 气候变暖
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Advances in landscape genomics and its application in integrated pest management

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Abstract: The recent development of novel sequencing technologies and bioinformatics has greatly

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facilitated the fundamental and applied studies on insect genomes with the steady increase of accomplishments. Studies that integrate variables of agricultural landscape with the genomic structure, genetically adaptive variation, and gene functions aid in better understanding of the molecular mechanisms associated with the adaptability and infestation of a target pest in a specific landscape framework, providing new thoughts and directions for pest management. Landscape genomics is an interdisciplinary subject combining landscape ecology with population genomics and aims to examine the genetic basis of adaptation of a given species to changing environments. Landscape genomics mainly focus on the investigation and analysis of adaptive evolution in species as well as gene flow and genetic drift among populations that are under environment-associated selection. The research methodology of landscape genomics can be generalized as the design of spatial sampling strategy, utilization of molecular markers, and data collection and analysis. In this article we reviewed the research status of landscape genomics including the major findings and achievements in recent years. Further, we elaborated the application and prospects of landscape genomics in the aspects of insecticide resistance management, conservation biological control, and integrated pest management in the context of global climate change, with the ultimate goal of reducing the use of insecticides and promoting the safe production of crops.

Key words: Landscape genomics; genetics; adaptation; evolution; transgenic crops; insecticide resistance; global warming

农业景观是一类比较特殊的景观，它不仅是包含了多种自然生境、多种土地利用类型、多种作物混合种植的复合农业生态系统，还频繁遭受人类的高强度干扰，时空格局呈现出复杂多变的特征（郑云开和尤民生，2009）。现代农业生产的集约化和规模化使得农田景观格局单一化以及自然天敌栖境的斑块化和破碎化，削弱了农田生态系统的服务功能，进而影响害虫的发生和危害（Veres *et al*., 2013；张永生等，2018；Li *et al*., 2020）。景观特征不仅影响害虫的分布及丰度，还能促进或者抑制害虫之间的基因流（Keller *et al*., 2013；Yadav *et al*., 2019），而基因流会影响物种的当地适应性（Caprio and Tabashnik, 1992；Edelaar and Bolnick, 2012）。与此同时，全球气候变暖也在加剧景观破碎化进程（Opdam and Wascher, 2004），并且会导致生物多样性的降低（Hoffmann and Sgro, 2011）和濒危物种的灭绝（Thomas and Kejariwal, 2004）。包括昆虫在内的生物通常采用改变适生区域或者适应本地环境（local adaptation）的策略来应对气候变暖（Aitken *et al*., 2008）。栖息地景观格局的改变、环境的异质性以及日益严重的气候变暖使得物种产生局部适应性，最终产生表型的适应性变异，这些变化可能会使得害虫的暴发更为频繁（Yadav *et al*., 2019）。除此之外，气候变暖使得害虫适生区扩张（Jepsen *et al*., 2011；Menéndez *et al*., 2014）、害虫与自然天敌在时间和空间上错位导致生物防控效率的降低（Van Nouhuys and Lei, 2004；Evans *et al*., 2013）以及三级营养关系互作（Rasmann *et al*., 2014）和抗药性（Op de Beeck *et al*., 2017）改变，对害虫综合治理措施提出了巨大的挑战。因此，从进化的角度理解害虫与天敌对气候变化的适应性，探索基于全球气候变化背景下的农业景观格局异质性对害虫种群适应性进化的影响，是研究害虫综合治理的重要方向。

在自然界，害虫的发生发展与“植物-害虫-天敌”三级营养关系以及周围的环境因素存在着错综复杂的联系。因此，害虫治理研究应以生态学原理和方法作为指导。传统的生态学研究大多集中在对物种的个体、种群、群落和生态系统等层面的表观特征，如性状、表型、行为和互作关系等，而要深入地了解这些表观特征背后的分子机理，并将其运用到害虫治理措施中，则需对物种的遗传组成、变异及其与所处环境之间的互作进行深入的研究（黄勇平和朱湘雄，2003）。景观基因组学（landscape genomics）为研究物种对空间和环境异质性的适应性进化提供了强有力的支持（Vincent *et al*., 2013）。由于基因组学的迅速发展，为景观遗传学的研究注入了新的动力，使得景观基因组学的研究得以发展。景观基因组学为基于农业景观背景下的害虫防治提供了一个很好的研究框架，基于景观基因组学的方法，可将农业景观中的生物及非生物因素（包括寄主类型及变异、景观要素、农事操作、气候因子等）与害虫的遗传变异结合分析，旨在揭示不同的农业景观格局

下害虫如何演化和适应当地的环境，为未来的害虫防治措施提供理论指导。

1　景观基因组学的研究范畴

景观基因组学把基因组学、生态学、空间分析方法与环境因子、景观要素结合起来分析，旨在揭示物种在基因组层面上的适应性遗传变异及其与环境异质性之间的关系（Manel *et al.*, 2010a; Schoville *et al.*, 2012; Bolliger *et al.*, 2014）。国际昆虫学界在2011 年提出了完成 5 000 种昆虫等节肢动物基因组测序计划（5 000 Insect Genome Project, i5K）（Robinson *et al.*, 2011），2012 年提出了 1 000 种昆虫转录组演化项目（1K Insect Transcriptome evolution, 1KITE）（www.1kite.org），以揭示昆虫对环境的适应性和遗传进化机制。测序技术的快速发展，目前已有 150 多种昆虫完成基因组测序和注释（Li *et al.*, 2019）。物种基因组及其相关信息的获取越来越高效和经济；地理信息系统和定位系统的日益完善也大大提高了空间数据的可获得性。基于这些技术以及景观遗传学的发展，景观基因组学的研究受到了越来越多研究者的关注，该学科主要研究景观特征或者气候因子对物种适应性遗传变异的塑造作用，探讨驱动物种对当地环境适应性的内在机制（图 1）（Joost *et al.*, 2007; Lowry, 2010; Manel *et al.*, 2010a）。

景观遗传学是将种群遗传学和景观生态学融合起来，旨在探索物种的种群间基因流、遗传不连续性和种群结构与景观和环境因子之间的关系，有助于理解物种的微进化过程（Manel *et al.*, 2003; Storfer *et al.*, 2007）。尽管景观基因组学属于景观遗传学的范畴，但是两者的主要研究内容有比较明显的区别。景观基因组学的研究重点在生物因子和非生物因子的变化对种群内遗传变异产生的影响（Manel *et al.*, 2010a）；景观遗传学的研究重点在生态过程，如景观变量（如道路、河流等）和非生物因素对物种扩散以及基因流的影响。根据遗传变异的分类，可将景观基因组学分为适应性景观基因组学和中性景观基因组学。适应性景观基因组学采用的分子数据主要是受选择作用的位点或者基因区域（适应性遗传变异），而中性景观基因组学采用的主要是不受选择作用的中性位点或者基因区域（中性遗传变异）（图 1）。目前景观基因组学的相关研究绝大部分都是关注于适应性景观基因组学，即研究物种受到环境因子的选择作用以及形成的适应性（表 1），因此我们以下综述和讨论更侧重于适应性景观基因组学方面的研究。中性景观基因组学与景观遗传学所关注的科学问题一样，重点在于群体之间的基因流以及遗传漂变（Rellstab *et al.*, 2015; Haasl and Payseur, 2016）。

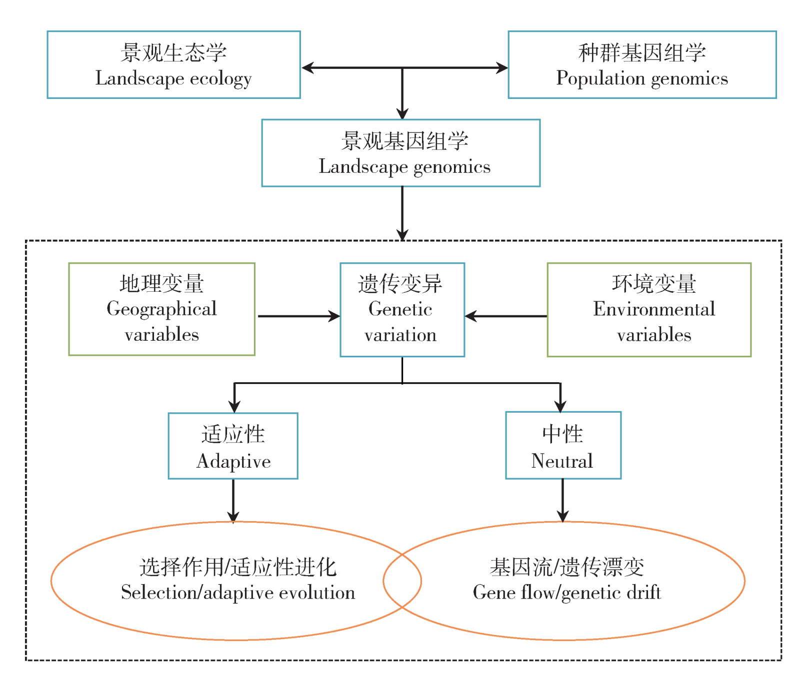


图 1　景观基因组学的理论框架及研究内容（改自 Balkenhol *et al.*, 2017）
Fig. 1　Conceptual framework and research focuses of landscape genomics (adapted from Balkenhol *et al.*, 2017)

表 1 景观基因组学研究中采用的分子标记、环境变量和分析方法

Table 1 Overview of molecular markers, environmental variables and statistical approaches applied in landscape genomics studies

类别 Category	物种 Species	分子标记 Molecular marker	环境变量 Environmental variable	Outlier 检测方法 Outlier detection method	基因-环境关联分析方法 Method for gene-environment association analysis	参考文献 References
植物 Plants	黄花棘豆 *Anthoxanthum odoratum*	AFLP	N, P, K, AN, pH	–	SAM	Freeland *et al*., 2010
	Arabis alpina	AFLP	C	–	GEE	Poncet *et al*., 2010
	火炬松 *Pinus taeda*	SSR, SNP	C	–	MLiR	Eckert *et al*., 2010b
	火炬松 *Pinus taeda*	SNP	C	–	Bayenv 1	Eckert *et al*., 2010a
	拟南芥 *Arabidopsis thaliana*	SNP	C, G	–	Partial Mantel test	Hancock *et al*., 2011
	黑云杉 *Picea mariana*	SNP	C	Arlequin, BayesFst	SAM	Prunier *et al*., 2011
	海岸松 *Pinus pinaster*	SNP	C, G	–	SAMc, MLiR	Grivet *et al*., 2011
	拟南芥 *Arabidopsis thaliana*	SNP	C	–	RDA	Lasky *et al*., 2012
	杨树 *Populus balsamifera*	SNP	C, G	–	Bayenv 1	Keller *et al*., 2012
	欧洲五针松 *Pinus cembra* 欧洲山松 *Pinus mugo* 欧洲银冷杉 *Abies alba* 欧洲落叶松 *Larix decidua*	SNP	C, G	–	Bayenv 1	Mosca *et al*., 2012
	Gentiana nivalis *Carex sempervirens*	AFLP	C, G	–	MLiR	Manel *et al*., 2012b
	Campanula barbata	AFLP	C	BayeScan, DFDIST	GLMs, GLMMs, GAMMs, CARTs	Jones *et al*., 2013
	Helianthus petiolaris	SNP	S, V	BayeScan	MR	Andrew and Rieseberg, 2013
	欧洲桤木 *Alnus glutinosa*	SNP	C	BayeScan	SAM, LFMM	De Kort *et al*., 2014
	Eucalyptus tricarpa	SNP	C	BayeScan	CsGoF	Steane *et al*., 2014
	蒺藜苜蓿 *Medicago truncatula*	SNP	C	–	TASSEL	Yoder *et al*., 2014
	白云杉 *Picea glauca* 恩氏云杉 *Picea engelmannii*	SNP	C	BayeScan	Bayenv 2	De La Torre *et al*., 2014
	毛果杨 *Populus trichocarpa*	SNP	C	–	Bayenv 2	Evans *et al*., 2014
	毛果杨 *Populus trichocarpa*	SNP	C, G	BayeScan, FDIST	Bayenv 2	Geraldes *et al*., 2014
	大麦 *Hordeum vulgare*	SNP	C, G	–	Bayenv 2, LFMM	Abebe *et al*., 2015
	欧洲云杉 *Picea abies*	SNP	C, G	–	Bayenv 2, Samβada	Ćalić, 2015
	Pinus lambertiana	SNP	C, G, S	–	Bayenv 2	Eckert *et al*., 2015
	Sphaeralcea ambigua	AFLP	C, G, WSI, TI	BayeScan	GDM	Shryock *et al*., 2015
	Aeonium davidbramwellii *Aeonium nobile*	ISSR	C	BayeScan	LFMM, Samβada	Harter *et al*., 2015
	Fagus sylvatica	SSR, SNP	C	–	LFMM	Pluess *et al*., 2016
	杜鹃花属 9 个种 Nine *Rhododendron* species	SSR	C, G, S, V	BayeScan, FDIST	Samßada	Huang *et al*., 2016
	Quercus lobata	SNP	C, G	–	RDA	Sork *et al*., 2016
	牛膝 *Achyranthes bidentata*	SCoT	C	BayeScan, Arlequin	LFMM, RDA	Yang *et al*., 2017
	垂枝桦 *Betula pendula*	SNP	C	–	RDA	Salojärvi *et al*., 2017
	Senecio hercynicus	AFLP	C	BayeScan, DFDIST	Samβada, partial db-RDA	Bog *et al*., 2017

续表 1 Table 1 continued

类别 Category	物种 Species	分子标记 Molecular marker	环境变量 Environmental variable	Outlier 检测方法 Outlier detection method	基因-环境关联分析方法 Method for gene-environment association analysis	参考文献 References
	大果铁杉 *Tsuga mertensiana*	SNP	C	–	RDA	Johnson *et al*., 2017
	Zea mays ssp. *parviglumis* *Zea mays* ssp. *mexicana*	SNP	C, G, S	–	Bayenv 2	Fustier *et al*., 2017
	Acacia koa	SNP	C, G	–	GFA	Gugger *et al*., 2017
	Biscutella laevigata	AFLP	G	–	GLMMs	Leempoel *et al*., 2018
	棕斑岩蔷薇 *Cistus ladanifer*	AFLP	F, D	BayeScan, MCHEZA	Samβada	Torres *et al*., 2018
	欧洲山毛榉 *Fagus sylvatica*	SNP	C, G	BayeScan, Arlequin, LOSITAN	Bayenv 2, Samβada	Cuervo-Alarcon *et al*., 2018
	蒺藜苜蓿 *Medicago truncatula*	SNP	C, S, A	–	LFMMs, MSOD-MSR	Guerrero *et al*., 2018
	舟山新木姜子 *Neolitsea sericea*	SNP	C	BayeScan	MLiR, GLMMs	Cao *et al*., 2018
	台湾杉 *Taiwania cryptomerioides*	AFLP, MSAP	C, G, S, V	BayeScan, DFDIST	GLMs, Samβada	Li *et al*., 2018
	越橘 *Vaccinium vitis-idaea*	SNP	C, PT	–	Samβada, CST, LFMM	Alam *et al*., 2018
	Corymbia calophylla	SNP	C	–	Bayenv2, Baypass, LFMM	Ahrens *et al*., 2019
	火炬松 *Pinus taeda*	SNP	C, G	SPA, OutFLANK	TASSEL, Samβada	Lu *et al*., 2019
	欧洲五针松 *Pinus cembra*	SNP	C	–	LFMM	Rellstab *et al*., 2019
	欧洲银冷杉 *Abies alba*	SNP	C, G, PT	BayeScan	Samβada, SAM, TASSEL	Konôpková *et al*., 2019
	Arabis alpina	SNP	C, SC	–	GLMM, LFMM	Lobréaux and Miquel, 2020
脊椎动物 Vertebrates	大西洋鳕鱼 *Gadus morhua*	SNP	C, SA, O	BayeScan, FDIST	Bayenv 2	Berg *et al*., 2015
	山羊 Goat	SNP	C, G	–	SAM	Pariset *et al*., 2009
	褐鳟 *Salmo trutta*	SSR	C, SA	Arlequin	SAM	Meier *et al*., 2011
	三刺鱼 *Gasterosteus aculeatus*	SSR, SNP	C, SA	BayeScan, LOSITAN	SAM, partial Mantel test	DeFaveri, 2013
	大西洋鲑鱼 *Salmo salar*	SNP	C, G, RP	–	RDA	Vincent *et al*., 2013
	虹鳟 *Oncorhynchus mykiss*	SNP	C, G, MD	–	ULR, DISTLM	Matala *et al*., 2014
	Oncorhynchus tshawytscha	SNP	C, G, MD, SO	–	RDA	Hecht *et al*., 2015
	多线南蜥 *Eutropis multifasciata*	SNP	C, G	–	BEDASSLE	Barley, 2015
	白胸鳾 *Sitta carolinensis*	SNP	C	BayeScan	Bayenv 2, LFMM	Manthey and Moyle, 2015
	Lagopus lagopus scotica	SNP	G, MR, PB	BayeScan, LOSITAN	Bayenv 2	Wenzel *et al*., 2016
	Ovis dalli dalli	SNP	C, G, FM	BayeScan, LOSITAN	Samβada	Roffler *et al*., 2016
	巴西猪 Brazilian swine	SNP	C	BayeScan	Samβada	Cesconeto *et al*., 2017
	Melanotaenia fluviatilis	SNP	C	–	RDA	Brauer *et al*., 2018
	山羊 Goat	SNP	C, G	–	SAM, Samβada	Mdladla *et al*., 2018
	白足鼠 *Peromyscus leucopus*	SNP	C, G	–	Pcadapt, LFMM	Garcia-Elfring *et al*., 2019

续表 1 Table 1 continued

类别 Category	物种 Species	分子标记 Molecular marker	环境变量 Environmental variable	Outlier 检测方法 Outlier detection method	基因-环境关联分析方法 Method for gene-environment association analysis	参考文献 References
	黄林莺 *Setophaga petechia xanthotera*	SNP	C, G, WSA	OutFLANK, BayeScan	BayeScEnv, LFMM, RDA	Chavarria-Pizarro *et al*., 2019
	达氏蟾头龟 *Mesoclemmys dahli*	SNP	FL	–	gINLAnd	Gallego-García *et al*., 2019
	田野林蛙 *Rana arvalis*	SNP	GSL	–	Pcadapt, LFMM	Rödin-Mörch *et al*., 2019
	人类 *Homo sapiens*	SNP	C	–	Bayenv2, LFMM	Igoshin *et al*., 2019
	黑鲍 *Haliotis rubra*	SNP	C, WE, OC, ST	–	LFMM, Baypass, RDA, GDM	Miller *et al*., 2019
无脊椎动物 Invertebrates	*Hylobius abietis*	AFLP	C, G	BayeScan, DFDIST	MLoR	Manel *et al*., 2009
	Aricia agestis	AFLP	CH, HT	BayeScan, DFDIST	Partial Mantel test, SGoF	Buckley *et al*., 2012
	大型溞 *Daphnia magna*	SSR, SNP	FA, LU, LC, PP	–	Partial Mantel test, RDA	Orsini *et al*., 2013a
	黄脊竹蝗 *Ceracris kiangsu*	AFLP	C	BayeScan, DFDIST	Samβada	Feng *et al*., 2015
	马铃薯甲虫 *Leptinotarsa decemlineata*	SNP	PI, PNH	–	LFMM, Baypass, BAYESCENV	Crossley *et al*., 2017
	西方蜜蜂 *Apis mellifera*	SNP	C, G	–	Samβada, LFMM, PCAdapt, his	Henriques *et al*., 2018
	东方蜜蜂 *Apis cerana*	SNP	G	–	Samβada	Montero-Mendieta *et al*., 2019
	Melipona subnitida	SNP	C, FC	–	LFMM	Jaffé *et al*., 2019
	7 种石蝇 Seven stonefly species	SNP	C, SC, WC, WT	–	LFMM, RDA	Gamboa and Watanabe, 2019
	Nyssorhynchus darlingi	SNP	FC	–	LFMM, Bayenv 2	Prussing *et al*., 2019
	Atta texana	SNP	C, FGC	–	BEDASSLE	Smith *et al*., 2019
	Phaulacridium vittatum	SNP	C, FPC, S, WS	OutFLANK, BayeScan	LFMM	Yadav *et al*., 2019

环境变量 Environmental variables: A: 大气变量 Atmospheric variables; AN: 添加的营养 Added nutrients; C: 气候变量 Climate variables; CH: 定殖历史 Colonization history; D: 干燥处理 Drought treatment; F: 火灾处理 Fire treatment; FA: 鱼类丰度 Fish abundance; FC: 森林覆盖度 Forest cover; FL: 森林减少程度 Forest loss; FM: 饲料指标 Forage metrics; FGC: 真菌基因型类群 Fungal genotypic cluster; FPC: 叶片投影盖度 Foliage projective cover; G: 地理变量 Geographic variables; GSL: 生长季节长度 Growing season length; HT: 生境类型 Habitat type; K: 钾 Potassium; LC: 土地覆盖分类 Land cover classes; LU: 土地开发强度 Land use intensity; MD: 迁移距离 Migration distance; MR: 用药情况 Medication regime; N: 氮 Nitrogen; O: 氧气浓度 Oxygen concentration; OC: 洋流 Ocean current; P: 磷 Phosphorus; PB: 寄生虫负荷 Parasite burden; PI: 马铃薯种植强度 Potato intensification; PP: 寄生虫的存在与否 Presence of parasites; PT: 表型性状 Phenotypic traits; PNH: 非森林生境比例 Percent nonforest habitat; RP: 河流属性 River properties; S: 土壤变量 Soil variables; SA: 盐度 Salinity; SC: 雪覆盖度 Snow cover; SO: 河流类别 Stream order; ST: 海平面温度 Sea surface temperature; TI: 热惯性 Thermal inertia; V: 植被变量 Vegetation variables; WE: 波动能量 Wave energy; WL: 水位 Water level; WSI: 水分胁迫系数 Water stress index; WS: 风速 Wind speed; WT: 水温 Water temperature; WSA: 水体盐度 Water salinity. 基因-环境关联分析方法 Gene-environment association: CART: 分类和回归树 Classification and regression trees; CST: 卡方检验 *Chi*-square test; CsGoF: 卡方拟合优度检验 *Chi*-square goodness-of-fit test; GDM: 广义相异模型 Generalized dissimilarity modelling; GEE: 广义估计方程 Generalized estimating equations; GFA: 森林梯度分析 Gradient forest analysis; GLMs: 广义线性模型 Generalized linear models; GAMM: 广义加性混合模型 Generalized additive mixed models; GLMMs: 广义线性混合模型 Generalized linear mixed models; MR: 多元回归 Multiple regression; MLiR: 多元线性回归 Multiple linear regressions; MLoR: 多元逻辑回归 Multiple logistic regressions; MSOD-MSR: Moran 光谱离群值检测/随机化 Moran spectral outlier detection/randomization; SGoF: 拟合优度法 Sequential goodness-of-fit method; ULR: 单变量线性回归 Univariate linear regression.

2 景观基因组学研究方法

2.1 空间采样策略

景观基因组学研究中的采样策略侧重于在不同的环境变量中进行梯度采样，如分别在不同的海拔高度对蜜蜂进行采样以推测其进化历史以及适应高海拔环境的候选基因(Montero-Mendieta *et al*., 2019)；分别在农业集约化程度不同的作物田采集马铃薯甲虫 *Leptinotarsa decemlineata* 以探究该害虫的抗药性演化(Crossley *et al*., 2017)。同时，在相似的目标环境因子中需进行重复采样，以减少假阳性的概率以及不同环境变量之间的协方差(Rellstab *et al*., 2015)。研究者也可以在特定区域进行大范围采样以覆盖研究物种的整个环境生态位，如对黄脊竹蝗 *Ceracris kiangsu* 在中国的分布区进行全面的采样(Feng *et al*., 2015)。基于充分的、可利用的生态和环境数据基础，运用模型进行环境因子的分层和模拟有利于采样策略的设计，以替代传统的随机采样(Manel *et al*., 2012a)，能够提高阳性位点的筛选效率(尤其是在弱选择作用的情况下)(Lotterhos and Whitlock, 2015)。根据生物在异质性景观中的有效扩散距离以及路径进行采样也是景观基因组学的重要考虑因素之一(Spear *et al*., 2010)，这样的采样方式能将遗传多样性与景观特征更好地关联起来。

采样策略的不同是景观基因组学和景观遗传学的重要区别之一。景观遗传学研究通常是根据影响物种基因流的环境变量进行采样设计，如沿着河流、山脉和道路对小菜蛾 *Plutella xylostella* 进行采样以分析这些景观因子对该害虫的遗传结构和基因流产生的影响(陈婷, 2015)；沿着河流的分支对淡水昆虫华丽色蟌 *Calopteryx splendens* 进行样本采集以探索陆地扩散和沿河流扩散两种方式对其种群遗传结构的影响(Chaput-Bardy *et al*., 2008)。

2.2 分子标记方法

景观基因组学需要足够多的分子标记覆盖整个基因组，包括了中性分子标记和适应性分子标记，其中适应性分子标记受到环境选择的压力，这有助于后续分析、理解物种对当地环境的适应性及其演化(Hansen *et al*., 2012)。多数景观遗传学使用数量较少的中性分子遗传标记[如简单重复序列(simple sequence repeat, SSR)]来分析环境因子与种群的空间遗传结构的关系(Joost *et al*., 2007; Manel and Holderegger, 2013; Berg *et al*., 2015)。中性遗传标记并不会受到选择作用的影响(Schwartz *et al*., 2010)，对于物种的存活、繁殖等个体适合度不产生影响，无法反映种群的适合度以及对环境的潜在适应能力(Holderegger and Wagner, 2006; Saccheri and Hanski, 2006)。目前，景观基因组学研究中所使用的分子标记主要包含两类：一是不包含 DNA 序列信息的分子标记，如扩增片段长度多态性(amplified fragment length polymorphism, AFLP)和目标起始密码子多态性(start codon targeted polymorphism, ScoT polymorphism)；二是包含序列信息的分子标记，如单核苷酸多态性(single-nucleotide polymorphisms, SNPs)。近年来，高通量测序技术(high-throughput sequencing, HTS)，又称为下一代测序技术(next-generation sequencing, NGS)的迅速发展，使得基于染色体序列的分子标记数据的获得更为经济和高效，这为探究种群多样性、种群遗传和物种在基因组水平上的适应性进化等方面提供了坚实的数据基础(Tautz *et al*., 2010; Davey *et al*., 2011)。因此，在景观基因组学研究中，覆盖全基因组的 SNP 分子标记应用越来越多(表 1)。

目前，基于全基因组重测序获得遗传标记信息所需的花费仍然较大，而简化基因组测序技术(reduced-representation genome sequencing, RRGS)作为一种高效的用于分子标记开发的测序技术，由于其花费小且不需要参考基因组信息而得到广泛运用(Miller *et al*., 2007; Andrews *et al*., 2016; Brauer *et al*., 2016)。简化基因组测序包括了基因分型测序(genotyping by sequencing, GBS)(Elshire *et al*., 2011)、与限制性核酸内切酶识别位点相关的 DNA 测序(restriction site-associated DNA sequencing, RAD-Seq)(Miller *et al*., 2007)和特异性位点扩增片段测序(specific-locus amplified fragment sequencing, SLAF-Seq)(Sun *et al*., 2013)等，其中 GBS 技术是 SNP 检测和分型的一种最新手段(Elshire *et al*., 2011)。除了 RRGS，混池测序(pool-sequencing)也是一种较为经济的测序方法，但是由于分析方法的限制，目前只有 Bayenv 2 能够分析全基因组混池测序所获得的遗传数据与环境数据之间的关系(Günther and Coop, 2013)，所以仅有少数的研究使用该方法(如：Turner *et al*., 2010; Fabian *et al*., 2012)。

2.3 数据分析方法

基因-环境关联分析(gene-environment association, GEA)是景观基因组学研究中主要的分析方法，通过分析物种基因组中的基因位点与特定的环境变量之

间的显著性关系，以研究这些异常位点在物种适应性进化过程中的作用（Joost *et al.*, 2007；Hancock *et al.*, 2011；Rellstab *et al.*, 2015）。在进行基因-环境关联分析之前，有研究者先进行异常位点的检测，再与环境因子做关联分析，广泛运用的软件包括 FDIST（Beaumont and Nichols, 1996）、BayeScan（Foll and Gaggiotti, 2008）、PCAdapt（Duforet-Frebourg *et al.*, 2014）、Arlequin（Excoffier *et al.*, 2009）、FLK（Bonhomme *et al.*, 2010）和 SPA（spatial ancestry analysis）（Yang *et al.*, 2012）（表 1）。目前使用得最多的是 BayeScan，该软件运用贝叶斯方法预估每个位点受到选择作用的可能性（Foll and Gaggiotti, 2008）。也有研究者直接将所有的分子标记位点与环境变量做相关分析（如：Mdladla *et al.*, 2018；Montero-Mendieta *et al.*, 2019）。环境因子主要包括气候数据、地理变量和土壤等生长环境数据等（表 1）。其中气候数据来源于当地气候数据网站以及全球气候数据网站，如 WorldClim（http://www.worldclim.org）。一般会尽可能地将所有可能性的环境因子加入到分析中，以检测到更多的适应性位点或者基因。在这些环境因子中，许多环境因子之间具有高度的相关性，如海拔和温度，纬度和太阳辐射。在基因-环境关联分析之前，通过主成分分析（principal component analysis, PCA）（如：Manel *et al.*, 2010b；Zulliger *et al.*, 2013）和方差膨胀因子（variance inflation factor, VIF）（如：Stucki *et al.*, 2017；Schmidt *et al.*, 2018）等方法找出引起多重共线性的环境变量，并将其剔除，再进行 GEA 分析。

目前，基因-环境关联分析方法主要包括 Bayenv 2（Günther and Coop, 2013）、潜在因素混合模型（latent factor mixed models, LFMM）（Frichot *et al.*, 2013）、Samβada（Stucki *et al.*, 2017）、空间分析方法（spatial analysis method, SAM）（Joost *et al.*, 2007）、Mantel 检验（Mantel test）（Mantel, 1967）、广义线性混合模型（generalized linear mixed model, GLMM）、多重线性回归分析（multiple linear regressions）和冗余分析（redundancy analysis, RDA）（Orsini *et al.*, 2013b）等（表 1）。其中，前 3 种模型（Bayenv 2, LFMM 和 Samβada）在景观基因组学研究中的应用最为广泛。Bayenv 2 是基于贝叶斯一般线性混合模型，用于分析校正后的等位基因频率和环境变量之间的关系（Coop *et al.*, 2010；Günther and Coop, 2013）。LFMM 模型是将种群遗传结构作为一个潜在的变量进行运算以降低假阳性信号（Frichot *et al.*, 2013；Caye *et al.*, 2016）。Samβada 使用逻辑斯蒂回归方程分析特定位点基因型与环境变量之间的关系，包括了单一变量模型和多变量逻辑回归模型（Stucki *et al.*, 2017）。为了降低假阳性率，通常使用多种方法联合进行与环境相关位点的检测与分析。

3 景观基因组学的研究现状

尽管在景观基因组学的概念提出后，这个研究方向引起了研究者们广泛的兴趣和关注，但是研究对象主要集中在植物和脊椎动物，针对无脊椎动物的研究相对较少（表 1）。植物具有较长的生活史以及自身的不可移动性，这些特性使其（尤其是树木）成为景观基因组学主要的研究对象，阐明生物对环境的适应性进化及其机制。Lu 等（2019）分析了火炬松 *Pinus taeda* 的 280 万个 SNP 与环境变量和地理变量之间的关系，发现经度、月最高气温和月降水量在火炬松的适应性遗传变异中起重要作用。进一步的研究将景观基因组分析与同质园的试验相结合，整合了基因组、表型和景观数据的方法，明确环境因子与物种的性状、遗传之间的关系。同质园试验（common garden trial）常用于测量来自不同气候地区的树木种群数量性状的适应性分化（Savolainen *et al.*, 2007；De Kort *et al.*, 2013）。De Kort 等（2014）将欧洲桤木 *Alnus glutinosa* 的 24 个欧洲群体进行同质园试验和景观基因组学研究，明确了温度和表型性状（如叶片大小）之间的关系，以及与受到温度选择作用的遗传位点之间的关系。景观基因组学研究还可为保护生物学和生态恢复提供遗传信息（Allendorf *et al.*, 2010），确定"保护单元"（conservation unit）以维持生物多样性以及为种质资源库提供信息（Breed *et al.*, 2013；Mijangos *et al.*, 2015）。Gugger 等（2017）利用简化基因组测序获得 311 棵金合欢 *Acacia koa* 的遗传信息，利用景观基因组学的方法分析出该树种的遗传结构与降雨量之间的显著关系，并且预测未来的气候变化会使得夏威夷岛的金合欢在遗传层面无法适应当地环境，这为制定种子转移计划提供了有利的信息。在对脊椎动物的研究中，主要集中在鱼类和家禽（表 1）。在鱼类的研究中，主要探究物种对自然环境的遗传适应性，为制定保护和管理野生种群提供有用的信息（Vincent *et al.*, 2013）。家禽除了受到生物和非生物因子的影响外，还受到人类和市场的影响，通过景观基因组学的方法将这些影响因素与基因组信息进

行分析，可以识别适合于特定环境的家禽基因型，这为家禽的遗传资源保护计划提供信息（Pariset *et al.*，2012）。如巴西猪适应性位点的等位基因频率表现出明显的区域差异，这与巴西南方和北方之间的温度、太阳辐射和降水方面的环境差异有关（Cesconeto *et al.*，2017）。

昆虫不同于植物和脊椎动物，世代时间短、繁殖力高，且具有主动扩散的能力，使得昆虫能够通过范围扩张应对环境变化（Menéndez，2007）。大多数昆虫分布范围广，沿着一定的环境梯度分布，通过物理特征的多态性和生理特性的变化，如孵化时间（Fält-Nardmann *et al.*，2016）、滞育（Moraiti *et al.*，2014）、化性（Yamanaka *et al.*，2008）、翅的形态（Rosetti and Remis，2018）和自身温度调控（Trullas *et al.*，2007）等来提高适合度以响应环境的梯度变化，而这些变化最终可能导致基因水平的适应性（Brisson，2010；Maeno and Tanaka，2010；Zhang *et al.*，2019）。这些特性使昆虫成为探究物种在不同环境条件下所产生的选择适应性的模式对象。

目前，有关昆虫对环境选择适应性方面的研究，主要集中在与自然环境梯度相关的适应性位点筛选（如：Feng *et al.*，2015；Henriques *et al.*，2018）和昆虫抗药性（如：Paris *et al.*，2010；Crossley *et al*，2017）。云南省和甘肃省高海拔地区的东方蜜蜂 *Apis cerana* 对高海拔环境产生适应性，在一系列与繁殖和取食行为相关的基因中产生了变异（Montero - Mendieta *et al.*，2019）。伊比利亚半岛的西方蜜蜂 *Apis mellifera* 有 140 个基因参与到对气候的适应性进化中（Henriques *et al.*，2018），而在害虫的相关研究中，如蝗虫 *Phaulacridium vittatum*，也发现了一些基因参与了对环境梯度的适应性（Yadav *et al.*，2019）。Crossley 等（2017）将作物集约化程度和非森林生境比例作为马铃薯甲虫抗药性进化的影响因素，分析了不同地理区域马铃薯甲虫种群抗药性相关基因核苷酸多样性，分析结果得出 11 个 SNP 与非森林生境比例相关，2 个 SNP 与作物集约化程度相关，38 个 SNP 与两个因素均相关。同时还筛选出 42 个候选抗药性基因，在小尺度范围内，种群的抗药性在 2 km 范围内具有异质性。

4　景观基因组学在害虫综合治理中的应用

展望未来，将景观基因组学应用到害虫治理的研究和规划中，有助于我们理解农业景观格局变化、气候变化与害虫综合治理的相互关系，进而为害虫持续控制提供理论和实践依据。景观基因组学在害虫综合治理中的应用主要包含以下 3 个方面。

4.1　抗药性治理

目前，已有超过 500 种昆虫对杀虫剂表现出不同程度的抗药性（Whalon *et al.*，2008；Tabashnik *et al.*，2014）。农业景观经常受到环境干扰，如农事操作和杀虫剂的使用，使得昆虫的空间分布也随之发生变化。与环境和害虫管理措施有关的选择压力对昆虫当地种群的遗传结构会产生影响（Thaler *et al.*，2008）。其中，杀虫剂的使用是害虫的抗药性基因受到选择作用的最主要因素，而且在景观尺度下显著影响害虫抗药性基因的遗传结构（Caprio，2001；Franck and Timm，2010），如 Franck 等（2007）认为来自法国、意大利、亚美尼亚（Armenia）和智利（Chile）的苹果蠹蛾 *Cydia pomonella* 的遗传结构不同与杀虫剂的使用有关。转基因抗虫作物的栽培能够显著降低化学杀虫剂的使用量，控制害虫的数量，提高作物的产量（Lu *et al.*，2012；Tabashnik *et al.*，2013）。但是转苏云金芽胞杆菌 *Bacillus thuringiensis*（Bt）基因作物长期大面积种植增加了目标害虫的受选择压力，导致目标害虫对转基因作物产生抗性，对其可持续发展造成潜在的威胁（Tabashnik *et al.*，2003，2008）。

杀虫剂的使用和转 Bt 基因作物的大面积种植使得昆虫产生抗药性，均是物种在高强度的选择压力下快速进化的典型例子，并且已经成为了当今公共安全和农业经济的重大问题之一。时间上和空间上的环境异质性影响生物适应性进化（如抗药性）的轨迹（Roux *et al.*，2008）。环境对害虫的选择压力呈现高度异质性，这与长期的害虫管理息息相关（REX Consortium，2013）。农业景观的破碎化以及农事操作使得选择压力呈现出异质性，且这异质性体现在一定的空间范围内（Paris *et al.*，2010；Sanford and Kelly，2011）。作物生境与非作物生境之间、转基因作物与庇护所之间的农药选择压力不同，使得害虫抗药性发展速率也不同。当不同斑块之间的连通性达到最佳的时候，物种的选择适应性因受到空间上或时间上的环境异质性影响而会有所延迟（Mani，1989；Caprio，2001；Kassen，2002）。作物生境与非作物生境之间（Mazzi and Dorn，2012）、转基因作物与庇护所之间（Tabashnik *et al.*，2012；Jin *et al.*，2015）的空间连通性可以保护害虫

的敏感种群,延缓害虫抗药性的发展。因此,应谨慎地设置不同生境之间的空间连通性以进行大尺度下的害虫管理(Fuentes-Contreras *et al.*, 2014)。实验证明施药处理的果园与周围未喷洒农药的寄主植物上的苹果蠹蛾种群之间频繁的基因流延缓了该害虫抗药性的发展(Basoalto *et al.*, 2010; Fuentes-Contreras *et al.*, 2014)。利用最佳的景观空间配置可延迟昆虫抗药性的发展,如庇护所与 Bt 棉花区域之间的距离为 0.75 km 时,最有利于棉红铃虫 *Pectinophora gossypiella* 抗药性的延迟(Carriere *et al.*, 2004)。但如何将空间尺度和时间尺度的选择压力与延迟或阻止抗药性进化过程相结合并没有达成共识(REX Consortium, 2013; Hackett and Bonsall, 2016, 2019)。

要合理进行作物田的空间管理,需要很好地理解害虫对作物田所使用农药/转基因作物的适应性以及在作物生境/转基因作物生境与非作物生境/庇护所之间的迁移所产生的基因交流。景观基因组学为研究害虫的遗传变异与农业景观中的害虫管理措施之间的关系提供了一个很好的框架,但是将其运用于农业害虫防治系统中的研究很少(Crossley *et al.*, 2017)。把景观基因组学运用于害虫抗药性治理的研究中,可将杀虫剂的使用种类、使用量、使用频率、其他农事操作以及景观要素等作为环境变量与害虫的抗药性基因变异进行 GEA 分析。通过景观基因组学筛选出的抗药性候选基因可能与历史用药有关,可利用 CRISPR/Cas9 技术或者 RNAi 技术对筛选出的候选基因进行功能验证,以明确候选基因参与介导害虫抗药性的分子机理。同时,基于景观基因组学的方法对庇护所进行评估,找到阻碍害虫对转基因作物产生适应性的有利屏障,合理设置庇护所的种植品种、种植模式和空间布局,如条带种植、镶嵌种植等,进而有效延缓目标害虫对转基因作物抗性的发展。例如,由于受到寄主植物的选择作用,为害非作物寄主艾叶 *Artemisia vulgaris* 和作物寄主玉米 *Zea mays* 的欧洲玉米螟 *Ostrinia nubilalis* 种群之间的基因交流受到限制,因此艾叶不适合作为延缓玉米螟抗 Bt 毒性的庇护所(Martel *et al.*, 2003)。通过研究害虫对转基因作物的适应性基因,以及庇护所对害虫适应性进化的延缓情况,为转基因作物的持续、合理种植提供依据。运用景观基因组学方法,筛选出与抗药性相关的候选基因,进行功能验证后,可对这些位点进行遗传监测(Manel *et al.*, 2003; Schwartz *et al.*, 2007; Hansen *et al.*, 2012)以期为化学农药的合理使用、转基因作物品种选择以及种植提供参考。

4.2 保护性生物防治

目前农业景观布局研究的核心技术是在连续的时空范围内对农业景观进行构建和设计,从景观格局上提高天敌生存活动的连续性,阻断害虫存活的时空连续性,最大限度地抑制害虫种群。景观组成通过连续的可利用栖境以及食物资源对基因流产生影响(Dreier *et al.*, 2014; Abdel Moniem *et al.*, 2016)。通过检测遗传变异,对害虫及其自然天敌的种群动态、基因流和对非作物生境寄主的适应性进行研究,从而判断非作物生境的植物是否适合用来增强天敌的繁衍和防控效能。

非作物生境是天敌避难的重要环境,尤其在田间施药或农事操作的时候(Gurr *et al.*, 2017; Heimoana *et al.*, 2017),能够提高天敌的多样性以及田间的害虫寄生率(Balmer *et al.*, 2013; Arnó *et al.*, 2018)。然而,并不是所有的非作物生境都能起到很好的保护与支持作用,如寄生蜂 *Trichogramma carverae* 会取食香雪球的花蜜,但只有白色香雪球能够显著地增加该寄生蜂的寿命和产卵量(Begum *et al.*, 2004)。自然天敌对非作物生境(蜜源)植物的选择与其对植物颜色和气味等的适应性进化有关(Chittka and Menzel, 1992)。Meyers(2011)证实了野生向日葵 *Helianthus annuus* 上的寄生蜂 *Dolichogenidea homoeosoma* 并不适应人工种植的向日葵,而野生向日葵与栽培向日葵上的寄生蜂之间存在高水平的基因流,从而限制了它对栽培向日葵的适应性以及对害虫向日葵螟 *Homoeosomae electellum* 的控制作用。基因流是物种适应性的一个根本原因,基因流的方向和速率是协同进化的一个重要影响因素(Crespi, 2000; Edelaar *et al.*, 2008; Edelaar and Bolnick, 2012)。当基因流的作用超过环境因子对物种的选择作用时,物种则无法产生当地的适应性(Crespi, 2000)。Lavandero 等(2011)通过对苹果园害虫苹果绵蚜 *Eriosoma lanigerum* 及其寄生蜂的基因流进行分析,认为活动于果树与非生境植物——欧洲火棘 *Pyracantha coccinea* 之间的苹果绵蚜蚜小蜂 *Aphelinus mali* 没有明显的遗传分化,具有一个较大的随机交配种群,并且也证实了存在阻碍害虫苹果绵蚜种群交流的天然地理屏障,欧洲火棘并不会成为苹果绵蚜的庇护所,因此该植物可以作为加强天敌控害能力的非生境植物。基于景观基因组学了解景观尺度下害虫与自然天敌的种群结

构、种群动态、基因流潜在的屏障以及对非寄主植物/猎物的适应性，可以为保护性生物防治(conservation biological control, CBC)提供更好、更持久的经济和环境可持续发展策略。

除了为自然天敌提供食物，CBC 还可以为其提供庇护场所，改善生存的微气候，如树篱可为自然天敌提供适宜的小气候及所需的资源(Pollard and Holland, 2006; Sánchez *et al*., 2010)。树篱对小气候的影响主要包括降低季风的影响(Ricci *et al*., 2009)和太阳的照射，提高了土壤的水分含量(Sánchez *et al*., 2010)，在夏天(Sánchez *et al*., 2010)和冬天(Pywell *et al*., 2005)为天敌提供更适宜的温度。在景观基因组学研究的基础上，结合气候预测，对生境进行合理化的管理，为天敌提供适宜的庇护场所，有助于其更好地适应气候变化。

4.3　全球气候变化对害虫治理的影响

理解物种如何适应环境变化是进化遗传学的主要内容之一。昆虫种群经常面临环境气候的快速变异，不同地理区域温度波动大，且随着气候变暖，大气温度持续上升(IPCC, 2014)。在这个持续升温的过程中，改变自身的遗传物质来响应温度的升高是昆虫应对气候变暖的策略之一(Menéndez, 2007)。为了适应全球气候变化导致的气温升高，果蝇体内某些染色体或基因发生了变异以增加自身的耐热性(Levitan and Etges, 2005)，且变异频率与温度升高幅度呈正相关(Balanya *et al*., 2006)。经过高温长期驯化后的果蝇呼出的二氧化碳明显增多，然而体内的能量代谢却没有明显的增加，是由于长期的高温压力下，果蝇的部分基因以及代谢通路发生了改变以适应温度的升高(Mallard *et al*., 2018)。

利用基因组学的方法，可以筛选出物种适应遗传的变异位点，并将其与物种的重要特性结合起来，如耐热性、翅展和体长等表型特点。在这个背景下，运用景观基因组学的方法可预测气候变化对于昆虫适应性等位基因频率及其基因流的影响。澳大利亚沿着纬度分布的蝗虫，体型大小与其中一些潜在适应性的基因位点相关，并且其中一个基因位点的等位基因频率沿着纬度呈现梯度性变化，这说明了沿着纬度梯度而变化的蝗虫体型可能具有适应性遗传的基础(Yadav *et al*., 2019)。目前许多生态学模型都有预测气候变暖背景下生物的潜在分布区，如 CLIMEX(Kriticos *et al*., 2015)和 MaxEnt(Phillips and Dudik, 2008)，但是在这些模型中并未考虑生物对于气候变化的适应性进化。发展基于景观基因组学的生态位模型有利于对昆虫的扩散区域进行更为有效的评估。通过预测时间和空间上景观格局的变化以及运用模型模拟在景观背景下生物的基因流，并把相应的过程或结果嵌入到生态学模型中，或者将物种的遗传变异(Fitzpatrick and Keller, 2014)与基于生理参数预测的种群适生性(如 CLIMEX 模型中的气候适生性指数)或者种群上升/下降趋势(Bay *et al*., 2018)相结合，能够更好地预测气候变化对生物潜在分布区的影响。基于景观基因组学，还可通过监测这些遗传物质的改变，寻找对害虫/自然天敌有害的遗传物质变化，并通过遗传防控技术(徐雪娇等, 2019)方式扩大/减少这种有害变异的影响，从而更为有效地进行害虫综合治理。

全球气候变暖不仅对昆虫种群产生直接的影响，而且可以通过营养级的相关物种(如寄主、天敌)产生直接或间接的作用，进而影响生物群落的组成和结构以及生态系统的服务功能(姚凤銮和尤民生, 2012)。昆虫和寄主植物对气候变暖的适应性响应不同，导致昆虫与寄主植物及其他营养级的关系发生改变，从而对害虫的种群、为害程度以及相应的防治措施产生影响。对于植食性昆虫，寄主植物的分布、可利用性、寿命和化学组成均是植食性昆虫种群遗传分化的主要影响因素(Egan and Ott, 2007; Toševski *et al*., 2015)。随着气候变暖的发生，二氧化碳浓度升高使得寄主植物中碳氮比增大而营养质量下降，植食性昆虫可能通过取食更多的食物以保证正常的生长发育(Stiling *et al*., 2002; Wolf *et al*., 2008)。而且，气温的升高使得昆虫世代数增加，这也将加剧昆虫的为害。然而，在协同进化过程中某些植食性昆虫可以通过调节自身的代谢等以适应寄主植物营养的改变，如蚜虫通过提高对氨基酸的利用以补偿寄主植物体内的营养下降(Sun *et al*., 2010)。在气候变暖条件下，营养级间的互作更为复杂。基于景观基因组学的方法，评估昆虫在不同的农业景观格局中所经历的环境选择作用以及适应性，筛选出昆虫与植物及其他营养级协同进化中的主要控制基因并推测主要的影响(气候)因子，为进一步通过基因编辑技术明确候选基因的功能奠定基础。这将为优化全球气候变化背景下的害虫综合治理策略提供更多依据。

5　小结与展望

景观基因组学融合了群体基因组学和景观生态

学，将环境因子和景观要素等作为影响因子，研究物种对环境的潜在适应性（Manel *et al.*, 2010a）。景观基因组研究中的采样策略主要是从不同的环境梯度进行采样以覆盖到更多的受选择群体。测序技术的发展使得研究人员能够获得覆盖整个基因组的分子标记，如 SNP。大量分析模型的开发，使得近几年来景观基因组学在研究植物和无脊椎动物对环境的适应性进化方面的研究得到广泛的应用，这些信息为植物和脊椎动物保护生物学方面提供了有利的信息。

虽然景观基因组学在物种对环境适应性的研究中已有广泛的运用，但是在害虫综合治理方面的应用仍然存在巨大的空白。生物进化在农业方面的研究已不再新奇，如作物育种、害虫抗药性的治理，但将土地利用以及景观的多样性等结合到农业生态系统的进化研究中仍鲜有报道（Thrall *et al.*, 2011; Crossley *et al.*, 2017）。理解景观尺度下，物种在基因组水平的选择和适应机制成为了重要挑战，这对于在大尺度范围进行害虫控制具有重要的作用，也可用于预测害虫防治方法（如杀虫剂的使用和转基因作物的种植）的可持续性。景观基因组学在害虫综合治理中具有相当大的应用前景，值得深入讨论和研究。

化学杀虫剂的不合理使用和转 Bt 作物的大面积种植使得害虫的抗性问题日益严峻。在不同的景观背景和农事操作下，害虫的抗性基因进化速率不同。景观基因组学为研究在异质性的农业景观中害虫对杀虫剂和转基因作物的抗性进化和基因流提供了强有力的工具，从而为杀虫剂的合理使用、景观要素的配置和庇护所的合理设置以稀释和延缓害虫抗性的发展提供指导。生物防治是害虫治理中不可或缺的一环。自然天敌对不同的非作物生境有不同的适应性（Meyers, 2011），且不同的景观组成对自然天敌在生境作物与非生境作物之间的扩散具有不同的阻隔或者促进作用（Lavandero *et al.*, 2011）。利用景观基因组学能够更好地评估非作物生境植物和景观格局等对自然天敌防控害虫的影响。害虫种群不仅要面对来自于人类的干扰和天敌的控制，还要面对自然环境的变化，尤其是气候变暖。在气温处于持续上升、极端气候频发的大环境下，害虫不得不改变自身的行为习性、栖息地和遗传物质（Deutsch *et al.*, 2008; Musolin and Saulich, 2012），以适应这种变化。将景观基因组学结合到生态位模型中能够更准确地预测害虫潜在适生区的变化。同时，基于景观基因组学的研究能够识别有利于害虫应对气候变化的基因位点或者区域，以期为害虫遗传防控技术提供理论指导。害虫处于"三级营养关系"的第二营养级，上行效应和下行效应均对自身产生影响，在气候变化背景下如何厘清这种错综复杂的关系是一种巨大的挑战。从景观基因组学的角度出发，找出"作物-害虫-天敌"三者协同进化的主要控制基因，可以为优化害虫治理策略提供理论基础。

尽管景观基因组学在害虫综合治理有巨大的潜在应用价值，但仍然面临着许多挑战。昆虫的可移动性使得研究者需要根据昆虫的活动能力以及景观格局制定采样计划，而合理的采样计划是后续分析的基础。通过景观基因组学的研究，筛选出来的候选基因存在假阳性的可能性，研究者可综合使用多个模型以及后期的基因功能验证以减少假阳性概率。在非模式生物中，由于基因信息的不完整，对基因功能验证仍然是一个巨大的挑战。随着越来越多分析模型的开发和测序技术的发展，会有越来越多的物种基因组被破译。尽管面临多种挑战，但凭借着景观生态学、基因组学在害虫综合治理中已有的研究和应用基础，以及先进的生物信息学方法，景观基因组学的进一步发展及其在害虫综合治理中的应用前景将会日益突显。

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